Research Article



Assessment of macroalgae coverage in a scarcely studied deep rocky reef in the tropical eastern Mexican Pacific

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ABSTRACT. The biodiversity of epibenthic communities in rocky reefs in the Mexican tropical Pacific has been studied minimally during the past three decades. This study describes the abundance and distribution of algae and invertebrates in a deep rocky reef from this region. Samples were taken at 20 m depth in 2012 by randomly placing 50×50 cm quadrats. Also, photographs were taken of each quadrat to quantify the coverage of organisms. Throughout the study, the algae were the most abundant group (17748.5 cm m⁻²), of which encrusting calcified (6350.9 cm m⁻²), turf (3040.3 cm m⁻²), and larger-sized articulated corallines (2700.9 cm m⁻²) had the highest coverage. Regarding invertebrates, zoanthids (1153.3 cm m⁻²) and corals (746.7 cm m⁻²) had high coverage. All of the algal groups were found on vertical and horizontal substrates. The detrended correspondence analysis showed that larger-sized articulated corallines and encrusting not calcified groups were prevalent on the horizontal substrate and corals on the vertical substrate. These abundance and distribution patterns represent the first quantitative study of rocky reefs from the region. Considering the rapid influence of human activities in this coastal zone and the fact that rocky reefs have been minimally studied, there is a clear need for long-term monitoring programs to establish reef communities' patterns and processes, which are useful in conservation programs.

Keywords: rocky reefs; deep subtidal communities; macroalgae; turfs; tropical marine biodiversity

INTRODUCTION

Rocky reefs comprise one of the most important ecosystems in coastal areas due to their high levels of biodiversity and productivity (Irving & Connell 2002, Piazzi et al. 2004, Balata & Piazzi 2008, Portugal et al. 2017, Spector & Edwards 2020). These ecosystems provide essential functions, serving as sites for larval dispersion, breeding, refuge, feeding, reproduction, recruitment, and habitat for economically significant species; they also provide numerous environmental services. For example, they supply habitat and food for other marine organisms, provide protection from disturbances for people, and support cultural services for tourists, recreational divers, and scientists, as well as their aesthetic value to photographers and other artists (Virgilio et al. 2006, Santander-Monsalvo et al. 2018, Hoffmann et al. 2022). In addition, they are economically valuable for fishing and tourism. However, the consequences of these activities have created pollution, habitat fragmentation, overfishing, the introduction of exotic species, sedimentation, diseases, and death (Santander-Monsalvo et al. 2018, Edwards & Konar 2020).

Rocky reefs have been studied around the world with diverse aims (Airoldi & Cinelli 1997, Barros et al.

Corresponding editor: Loretto Contreras

2001, Piazzi & Cinelli 2001, Piazzi et al. 2002, Balata et al. 2006, 2007a,b, Wernberg & Connell 2008, Glasby et al. 2017, Cordero-Umaña & Santidrián-Tomillo 2020, Bell et al. 2022, Canessa et al. 2022, Martinez et al. 2022). Reef ecosystems are widely distributed throughout Mexico's temperate and tropical coastal areas. They are ecologically important; almost half of them are protected by the federal government under the Natural Protected Area scheme. Coral reefs are more commonly protected under this system, while the rocky reefs of the Pacific coast are excluded, specifically those located in the tropical Pacific region (Santander-Monsalvo et al. 2018). In coastal areas in the Mexican Pacific, the greatest number of studies have been performed in the temperate and temperate-tropical transition regions (Carreón-Palau et al. 2003, Casas-Valdéz & Aguila-Ramírez 2008, Castañeda-Fernández et al. 2010, Ulate et al. 2016, Favoretto et al. 2022). In the tropical region, studies have been performed mainly in rocky intertidal and shallow subtidal areas (León-Tejera & González-González 1994, Mendoza-González & Mateo-Cid 1998, Ávila-Ortiz & Pedroche 2005, Rodríguez et al. 2008, Mendoza-González et al. 2011, Mateo-Cid & Mendoza-González 2012, Mendoza-González et al. 2018), mostly with a floristic or taxonomic approach, leaving deep rocky reefs essentially unexplored, principally due to logistical and funding limitations.

Hence, these ecosystems are practically unknown in the Mexican tropical Pacific, specifically in Zihuatanejo's coastal areas. Salcedo-Martínez et al. (1988) carried out an inventory of macroalgae and invertebrates at nine locations in Zihuatanejo, six of which were rocky reefs, including the Sacramento deep rocky reef. Other research carried out in El Yunque, and La Ropa reefs described the structure of the macroalgal community (López et al. 2000) and the morphological variations of algal turfs (López et al. 2004). Therefore, this preliminary study aimed at determining the abundance and distribution of the epibenthic organisms on the Sacramento deep rocky reef.

MATERIALS AND METHODS

Study area

The study was carried out on the NW end of Bajo Sacramento (17°38'02"N, 101°36'39"W), located 3 km south of Ixtapa Bay, Guerrero State, Mexico (Fig. 1).

The climate is Aw, a warm sub-humid with summer rainfall (García 2004) with an average annual temperature of 25°C and an annual rainfall of 800-1600 mm. The predominant winds are SE in the rainy season and NW during the dry season. The Sacramento rocky reef is characterized by a pinnacle that emerges above the sea surface with vertical walls with a 70-90° slope; at a depth of 10 m, an extensive platform is formed that descends to a depth of 30 m. The topography in this zone is heterogeneous, and the bottom is composed of overlapping, irregularly shaped rocky blocks 1-5 m long, among which there are sand, gravel, and boulders deposits. The biggest rocks are cube-shaped with relatively flat upper faces. The smaller blocks exhibit a more irregular morphology. The site is exposed to strong internal currents, which produce laminar or turbulent flows of water that are stronger during the rainy and hurricane seasons.

Sampling

This study was performed in January, June, and October 2012 via SCUBA diving at 20 m depth. For each date, six 50×50 cm quadrats divided into 10×10 cm sub-quadrats were randomly placed on both vertical and horizontal substrates. Because of difficult environmental conditions, we could not sample two quadrats; thus, 16 quadrats were sampled (10 on the horizontal substrate and 6 on the vertical). Three 10×10 cm macroalgae samples were randomly collected by hand from each 50×50 cm quadrat using a hammer and chisel. In June, the adverse weather conditions did not allow the collection of samples; only photographs were taken. Samples were placed in plastic bags and taken to the laboratory for processing and taxonomic identification. The algal material was preserved in 4% formalin seawater.

All macroalgal species were identified following Dawson (1953, 1954, 1960, 1961, 1962, 1963a,b) and Taylor (1945). Photographs of each sub-quadrat (10×10 cm) of each quadrat (50×50 cm) were taken with a Canon 10, 15 MG camera to quantify the algal cover (cm m^{-2}). The algal cover was quantified by classifying morphological functional groups (Balata et al. 2011). This classification proposal results from the subdivision of the morphological functional groups of Steneck & Dethier (1994) based on the structure of the thallus, growth form, branching pattern, and taxonomic affinities. This expanded classification allowed the morphological functional groups to be quantified straightforwardly and reliably, corresponding with specific algal genera. Additionally, we included turf growth form as a useful descriptor of the assemblages of benthic organisms, which many authors around the world have employed because of its prevalence in benthic assemblages (Kendrick 1991, Airoldi 1998, 2000, Cheroske et al. 2000, Irving & Connell 2002,



Figure 1. Study area. The upper map shows the location of Ixtapa-Zihuatanejo in Guerrero State. The lower map shows the location of Sacramento in Ixtapa-Zihuatanejo.

Coleman 2002, 2003, Prathep et al. 2003, Birrell et al. 2004, Kelaher & Castilla 2005, Batelli & Rindi 2008, Connell et al. 2014, Gowan et al. 2014, Harris et al. 2015, Short et al. 2015, Martins et al. 2016, López et al. 2017). We have also included the "tassel" category because it is very common in our study site. However, it has not been described in any previous classification. A tassel forms tufts composed of very thin, abundant filaments of cyanoprokaryotic algae with an intense red color and a soft texture. Because the presence of some macroinvertebrates was conspicuous, the coverage of large taxa such as Porifera (PO), Echinoidea, e.g. sea urchins (SU), Octocorallia-Alcyonacea (CO), Zoanthidae (ZO) and Ascidiacea (AS) was included (Brusca 1983). In cases when some epibiotic component could not be identified from a photograph, it was referred to as "unidentified" to quantify its coverage.

Statistical analysis

Based on the Kruskal-Wallis (K-W) test statistic, the significant differences between the coverages of morphological, functional groups of macroalgae were demonstrated for each substrate. Certain functional groups were not detectable on some sampling dates, so no differences were recorded. Different groups of organisms were used as ordering variables for the sampling quadrats to determine their significance based on the coverage in the two substrates studied. Using detrended correspondence analysis (DCA) (Hill & Gauch 1980, Gauch 1982) and the DECORANA program (PC-ORD 5), the different sampling quadrats obtained from the horizontal (H) and vertical (V) substrates during the year were ordered in a multidimensional space. Each quadrat is identified according to the coverage of the morphological functional groups of macroalgae.

RESULTS

From the total quadrats analyzed, 42 species of macroalgae were identified (Table 1), 29 Rhodophyta, 8 Chlorophyta, 5 Ochrophyta-Phaeophyceae, and 1 Cyanobacteria. These included the following morphological functional groups: encrusting calcified (EC), prostrate not strictly adherent to the substratum (PS), larger-sized articulated corallines (AR), encrusting not calcified (ENC), encrusting (ER), turf-forming algae (TU) and tassel (TA) (Table 1).

No significant differences were observed among study dates for many of the algal functional groups and

Table 1. Functional group of algal species and taxa of invertebrates of the Sa	cramento rocky reef.
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Taxa	Functional	Таха	Functional
Таха	group	Таха	group
Rhodophyta		Chlorophyta	
Acrochaetium sp.	TU	Boodleopsis sp.	TU
Amphiroa beauvoisii	AR	Bryopsis pennata	TU
Amphiroa misakiensis	AR	Chaetomorpha antennina	TU
Amphiroa rigida	AR	Chlorodesmis sp.	TU
Asparagopsis taxiformis	TU	Cladophora microcladioides	TU
Ceramium affine	TU	Cladophora glomerata	TU
Ceramium zacae	TU	Derbesia marina	TU
Ceratodictyon tenue	TU	Derbesia tenuissima	TU
Champia parvula	TU	Ochrophyta-Phaeophyceae	
Dasya sinicola var. abyssicola	TU	Dictyopteris delicatula	TU
Erythrotrichia carnea	TU	Lobophora variegata	PS
Gelidium pusillum	TU	Neoralfsia sp.	ER
Gracilaria sp.	TU	Ralfsia pacifica	ER
Halichrysis sp.	TU	Sphacelaria rigidula	TU
Halymenia cf abyssicola	TU	Cyanoprokaryota	
Herposiphonia litoralis	TU	Oscillatoriaceae	ТА
Herposiphonia secunda	TU	Invertebrate taxa	
Hildenbrandia sp.	ENC	Porifera	РО
Hypnea pannosa	TU	Echinoidea (sea urchins)	SU
Hypnea johnstonii	TU	Octocorallia (Alcyonacea)	CO
Jania subpinnata	TU	Zoanthidae	ZO
Lejolisia colombiana	TU	Ascidiacea	AS
Lithophyllum sp.	EC		
Parviphycus antipae	TU		
Peyssonnelia rubra	PS		
Polysiphonia subtilissima	TU		
Porphyra sp.	TU		
Pterocladiella caloglossoides	TU		

invertebrate groups. Only significant differences in the H substrate for the EC group (KW-H_(2, 9) = 5.8; P = 0.05) with a median of 4930 cm m⁻² in January, 1840 cm m⁻² in June and 3980 cm m⁻² in October (Fig. 2), and marginal differences for the AR group (KW-H_(2, 9) = 5.5; P = 0.06) with a median of 1784 cm m⁻² in January, 2500 cm m⁻² in June, and 1090 cm m⁻² in October (Fig. 3).

An annual analysis of coverage variations was developed for the algal functional groups and invertebrate taxa by comparing both substrates. Only significant differences between H and V substrate for AR (KW-H_(1, 15) = 3.55; P = 0.05) were observed, with a median for the H substrate of 2068 cm m⁻² and the V substrate of 930 cm m⁻² (Fig. 4).

Similarly, significant differences in the TA group (KW-H_(1, 7) = 4.58; P = 0.03) with a median for the H substrate of 486 cm m⁻² and the V substrate of 20 cm m⁻² were observed (Fig. 5).

Finally, a group of invertebrates was observed, CO group (KW-H_(1,8) = 3.8; P = 0.05) with a median for the H substrate of 20 cm m⁻², and the V substrate of 620 cm m⁻² (Fig. 6).

Several groups of macroalgae had notably different mean annual coverage values in the two substrates. TU and AR exhibited twice as much coverage on the H substrate compared to the V, and TA also showed very high coverage on the H. At the same time, it had the lowest coverage on the V substrate (Table 2). The ENC and ER groups of macroalgae exhibited double the coverage on the V substrate. The mean annual coverage of CO was high on the V substrate but very low on the H (Table 2).

The DCA ordered the samples and organism groups according to the substrate inclination. AR and ENC were characteristic of the H substrate (Kendall Tau = 0.70 and 0.54, respectively). The CO was distributed on the V substrate (Kendall Tau = 0.68 and 0.57) (Fig. 7).



Figure 2. Coverage temporal variation of encrusting calcified (EC) on the horizontal substrate.



Figure 4. Total coverage of articulated corallines (AR) on the horizontal (H) and vertical (V) substrates.



Figure 3. Coverage temporal variation of articulated corallines (AR) on the horizontal substrate.



Figure 5. Total coverage of tassel algae (TA) on the horizontal (H) and vertical (V) substrates.



Figure 6. Total coverage of coral (CO) on the horizontal (H) and vertical (V) substrates.

Table 2. Average annual coverage and standard error of epibenthic organisms on horizontal and vertical substrates. *Samples from these groups were not collected. **Standard error was not obtained. PO: Porifera, SU: sea urchins, CO: Octocorallia-Alcyonacea, ZO: Zoanthidae, AS: Ascidiacea, EC: encrusting calcified, PS: prostrate not strictly adherent to the substratum, AR: larger-sized articulated corallines, ENC: encrusting not calcified, TU: turf-forming algae, TA: tassel, ER: encrusting.

Algae functional groups	Horizontal substrate	Vertical substrate
/invertebrate groups	$(cm m^{-2})$	$(cm m^{-2})$
AR	1780.9 ± 295.2	920.0 ± 105.6
TU	2003.6 ± 294.5	1036.7 ± 527.9
EC	3377.6 ± 607.7	2973.3 ± 372.4
PS	914.7 ± 249.0	1307.0 ± 338.1
ENC	453.3 ± 213.6	980.0 ± **
ER	366.7 ± 77.2	900.0 ± 235.7
TA	708.0 ± 332.2	26.7 ± 6.7
РО	352.0 ± 90.7	164.0 ± 71.9
SU	120.0 ± 46.2	*
CO	86.7 ± 66.7	660.0 ± 230.1
AS	$20.0 \pm **$	*
ZO	*	1153.3 ± 673.3
UN	148.0 ± 90.7	496.0 ± 247.8
Total	10331.5	10617.3

The DCA explained a variation with 0.88 inertia; the first axis contributed with a 0.27 eigenvalue, and the second axis with a 0.09 eigenvalue.

Figure 7 shows a larger number of quadrats placed on the horizontal bedrock clustered to the right of axis 1 in the eigenvector AR, while the other set of quadrats placed on the vertical bedrock, along with some from the horizontal bedrock, cluster to the upper right of the axis around the CO eigenvectors.

DISCUSSION

This work showed that the Sacramento rocky reef comprises a habitat that harbors significant algae biodiversity that was little known until now. Forty-two species of macroalgae were identified, exceeding the last number recorded in an inventory-type study of Sacramento (Salcedo-Martínez et al. 1988). They recorded just two species of macroalgae on the reef, *Halimeda discoidea* at 7 m depth and *Lithophyllum* sp. (reported as *Lithothamnium* sp.) at 25 m depth. The other rocky reef studied in the Zihuatanejo region is El Yunque, located 9 km from Sacramento with a depth of 12 m (López 1993, 1996, López et al. 2000).

The total number of macroalgae species in El Yunque was 38. Seventeen of these were also found in

this work, including Amphiroa misakiensis, A. beauvoisii, A. rigida, Champia parvula, Hypnea pannosa, Cladophora microcladioides, Derbesia marina, Dictyopteris delicatula, Lobophora variegata, and Ralfsia pacifica.

The general pattern of coverage of organisms showed that algae were predominant throughout the study site, which contrasts with the low coverage of invertebrates. Based on their high coverage, the predominant algal functional groups were EC, TU, and AR. These groups and their representative taxa have also been found on other rocky reefs, mainly in the Mediterranean Sea (Airoldi & Virgilio 1998, Balata et al. 2005, 2006, 2007a, 2011, Virgilio et al. 2006). The encrusting calcified algae have a wide distribution in rocky littoral areas, from the intertidal and shallow subtidal zones up to 200 m deep. They are among the most abundant organisms on hard substrates with strong currents. Illumination is less than 0.1% surface (Steneck 1986, Björk et al. 2005). Although current and illumination were not measured at Sacramento, the wide distribution pattern in the V and H substrates and the high coverage of these algae coincide with reports from other regions. Therefore it is necessary to include these factors in subsequent studies to determine their influence.

The TU was the other predominant algal group based on coverage. In contrast to turfs described for other coastal areas around the world in which species such as Womersleyella setacea (Batelli & Rindi 2008) or a functional group like filamentous algae (Kendrick 1991, Airoldi et al. 1995) are predominant, the Sacramento rocky reef turfs are composed of multiple species of Rhodophyta, Chlorophyta, Phaeophyceae, and Cyanobacteria. There is no predominant species, functional group, or growth form. The TU at Sacramento had a height of <5 mm, agreeing with the only previous regional report from the coral reef at Las Gatas Beach (López et al. 2017). The algal turf species observed can be grouped within the algal functional groups proposed by Balata et al. (2011). Ceramium spp. and Cladophora spp. are grouped in filamentous algae, Amphiroa spp. in articulated algae, Lithophyllum sp. and Neoralfsia sp. are grouped into calcified encrusting algae, and noncalcified encrusting algae, respectively. Hypnea pannosa and Champia parvula belong to the group of corticate algae. The lack of previous studies of the Sacramento rocky reef does not permit a more detailed comparison of the algal turfs. The previously mentioned study at the El Yunque rocky reef was a floristic work that did not include functional groups or growth forms. The turfs are widely distributed in nume-



Figure 7. Detrended correspondence analysis (DCA) for the samples of algal functional groups and taxa of invertebrates on the horizontal (H) and vertical (V) substrates. PO: Porifera, SU: sea urchins, CO: Octocorallia-Alcyonacea, ZO: Zoanthidae, AS: Ascidiacea, EC: encrusting calcified, PS: prostrate not strictly adherent to the substratum, AR: larger-sized articulated corallines, ENC: encrusting not calcified, TU: turf-forming algae, TA: tassel, ER: encrusting.

rous temperate (Antoniadou & Chintiroglou 2005, Balata et al. 2005, Wallenstein et al. 2008) and tropical (Hay 1981, Birrell et al. 2004, Gowan et al. 2014, Sura et al. 2019) coastal areas. Their presence is mainly attributed to high concentrations of sedimentation and nutrients and reduced herbivory (Sura et al. 2019). In Sacramento, these factors may play an important role in the distribution and abundance of this algal growth.

Regarding the invertebrates, it was notable that ZO was only found on the vertical substrate, in contrast to SU and AS, which were found only on the horizontal. In other deep ecosystems, such as the biogenic reefs in the Mediterranean, it has also been found that specific communities of organisms exist as a function of the incline of the substrate (Cocito et al. 2002, Piazzi et al. 2002, Virgilio et al. 2006). The invertebrate taxa reported in this study agreed with reports from other temperate rocky and coralligenous locations (Balata et al. 2005). The deep, rocky habitats of the Mexican Pacific are practically unstudied, as compared to those in temperate regions, where it has been determined that various physical factors influence the diversity of organisms as sedimentation, hydrodynamics, nutrients, the slope of the substrate, and topography (Antoniadou

& Chintiroglou 2005, Balata et al. 2006, 2007a). These factors vary as a function of depth. In most sublittoral ecosystems, it is a common phenomenon that determines the structure of the assemblages (Garrabou et al. 2002, Bell et al. 2022), e.g. water movement is significantly less in deep water, up to 25-30 m, than in shallow water.

Furthermore, physical factors have a combined effect on the epibenthic organisms, e.g. the geomorphological characteristics of the site determine the influence of the water movement among microenvironments. Similarly, biotic interactions significantly influence the abundance and distribution of organisms in the deep environment (Bell et al. 2022, Canessa et al. 2022), such as competition for space. An important structuring mechanism in rocky reef communities in which organisms with different types of nutrition limit their growth rates. For example, photosynthetic organisms deprive feeders of suspended particulate organic matter, while suspension feeders deprive photosynthetic organisms of light (Ballesteros 2006).

This study allowed us to recognize which groups of organisms are typical of V and H substrates, as evidenced in the DCA. Differences in the slope of the substrate could cause variations of some abiotic factors such as light and sedimentation (Cocito et al. 2002, Irving & Connell 2002). Light incidence, substrate inclination (Antoniadou & Chintiroglou 2005), and sedimentation (Balata et al. 2005) are higher on horizontal surfaces than vertical ones, favoring an increase in photosynthetic organisms such as those that form algal turfs. Such factors could play a significant role in the structure of assemblages at Sacramento, as demonstrated in rocky (Bell et al. 2022) and biogenic reefs (Ballesteros 2006).

Sacramento had not been studied for three decades. Moreover, there is an information gap of almost 20 years on rocky reefs in the Mexican tropical Pacific region. Due to the serious threats provoked by human activity, it is essential to continue developing research to determine the processes that organize the assemblages of organisms.

Finally, this work represents the first quantitative reference of the epibenthic flora and fauna of a deep rocky reef in the Mexican tropical Pacific region. From this study, it is clear that focused exhaustive research is needed to determine the spatial and temporal patterns of assemblages of organisms and the mechanisms that structure them.

ACKNOWLEDGMENTS

We thank the Facultad de Ciencias, Universidad Nacional Autónoma de México, for partial financial support and for providing the infrastructure for the study. To Nick Wolf for translating the manuscript into English, to Mr. Thierry Durand for the diving service for the sampling. To Alejandra Sandoval Coronado for her help in editing the manuscript.

REFERENCES

- Airoldi, L. 1998. Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. Ecology, 79: 2759-2770. doi: 10.1890/0012-9658(1998)079[2759:RODSSA]2.0.CO;2
- Airoldi, L. 2000. Effects of disturbance, life histories, and overgrowth on the coexistence of algal crusts and turfs. Ecology, 81: 798-814. doi: 10.1890/0012-9658(2000) 081[0798:EODLHA]2.0.CO;2
- Airoldi, L. & Cinelli, F. 1997. Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a Mediterranean rocky shore. Journal of Experimental Marine Biology and Ecology, 215: 269-288. doi: 10.1016/S0022-0981(96)02770-0

- Airoldi, L. & Virgilio, M. 1998. Responses of turfforming algae to spatial variations in the deposition of sediments. Marine Ecology Progress Series, 165: 271-282. doi: 10.3354/meps165271
- Airoldi, L., Rindi, F. & Cinelli, F. 1995. Structure, seasonal dynamics and reproductive phenology of filamentous turf assemblage on a sediment influenced, rocky subtidal shore. Botanica Marina, 38: 227-237. doi: 10.1515/botm.1995.38.1-6.227
- Antoniadou, C. & Chintiroglou, C. 2005. Biodiversity of zoobenthic hard-substrate sublittoral communities in the Eastern Mediterranean (North Aegean Sea). Estuarine, Coastal and Shelf Science, 62: 637-653. doi: 10.1016/j.ecss.2004.09.032
- Avila-Ortiz, A. & Pedroche, F.F. 2005. El género Padina (Dictyotaceae, Phaeophyceae) en la región tropical del Pacífico mexicano. Monografías Ficológicas, 2: 139-171.
- Balata, D. & Piazzi, L. 2008. Patterns of diversity in rocky subtidal macroalgal assemblages concerning depth.
 Botanica Marina, 51: 454-471. doi: 10.1515/BOT. 2008.068
- Balata, D., Acunto, S. & Cinelli, F. 2006. Spatio-temporal variability and vertical distribution of a low rocky subtidal in the north-west Mediterranean. Estuarine, Coastal and Shelf Science, 67: 553-561. doi: 10.1016/ j.ecss.2005.12.009
- Balata, D., Piazzi, L. & Benedetti-Cecchi, L. 2007b. Sediment disturbance and loss of beta diversity on subtidal rocky reefs. Ecology, 88: 2455-2461. doi: 10.1890/07-0053.1
- Balata, D., Piazzi, L. & Cinelli, F. 2007a. Increase of sedimentation in a subtidal system: effects on the structure and diversity of macroalgal assemblages. Experimental Marine Biology and Ecology, 351: 73-82. doi: 10.1016/j.jembe.2007.06.019
- Balata, D., Piazzi, L. & Rindi, F. 2011. Testing a new classification of morphological functional groups of marine macroalgae for the detection of responses to stress. Marine Biology, 158: 2459-2469. doi: 10.1007/S00227-011-1747-Y
- Balata, D., Piazzi, L., Cecchi, E. & Cinelli, F. 2005. Variability of Mediterranean coralligenous assemblages subject to local variation in sediment deposition. Marine Environmental Research, 60: 403-421. doi: 10.1016/j.marenvres.2004.12.005
- Ballesteros, E. 2006. Mediterranean coralligenous assemblages: a synthesis of present knowledge. Oceanography and Marine Biology, 44: 123-195. doi: 10.1201/9781420006391-7

- Barros, F., Underwood, A.J. & Lindegarth, M. 2001. The influence of rocky reefs on the structure of benthic macrofauna in nearby soft sediments. Estuarine, Coastal and Shelf Science, 52: 191-199. doi: 10.1006/ ecss.2000.0734
- Batelli, C. & Rindi, F. 2008. The extensive development of the turf-forming red alga *Womersleyella setacea* (Hollenberg) R.E. Norris (Rhodophyta, Ceramiales) in the Bay of Boka Kotorska, Montenegro (southern Adriatic Sea). Plant Biosystems, 142: 120-125. doi: 10.1080/11263500701872747
- Bell, J.J., Micaroni, V., Harris, B., Strano, F., Broadribb, M. & Rogers, A. 2022. Global status, impacts, and management of rocky temperate mesophotic ecosystems. Conservation Biology, e13945. doi: 10.1111/ cobi.13945
- Birrell, C.L., McCook, J.L. & Willis, B.L. 2004. Effects of algal turfs and sediment on coral settlement. Marine Pollution Bulletin, 51: 408-414. doi: 10.1016/j.marpolbul.2004.10.022
- Björk, M., Mzee-Mohammed, S., Björklund, M. & Semesi, A. 2005. Coralline algae, important coral-reef builders threatened by pollution. AMBIO A Journal of the Human Environment, 24: 502-505.
- Brusca, R.C. 1983 Common intertidal invertebrates. University of Arizona Press, Arizona.
- Canessa, M., Bavestrello, G., Guidetti, P., Navone, A. & Trainito, E. 2022. Marine rocky reef assemblages and lithological properties of substrates are connected at different ecological levels. European Zoological Journal, 89: 813-826. doi: 10.1080/24750263.2022. 2095045
- Carreón-Palau, L., Guzmán-del Proó, S.A., Belmar-Pérez, J., Carrillo-Laguna, J. & Herrera-Fragoso, R. 2003. Microhabitat and associated biota of abalone juveniles, *Haliotis fulgens* and *H. corrugata*, in Bahía Tortugas, Baja California Sur, Mexico. Ciencias Marinas, 29: 325-341. doi: 10.7773/cm.v29i3.153
- Casas-Valdéz, M. & Aguila-Ramírez, R.N. 2008. Spatial variation of biomass of seaweed assemblages in the temperate-tropical transition zone of Baja California Peninsula, Mexico. Hidrobiologica, 18: 137-146.
- Castañeda-Fernández de Lara, V., Reyes-Bonilla, H. & Serviere-Zaragoza, E. 2010. A tropical assemblage of benthic macroalgae on rocky reefs in a temperate zone on the western Baja California peninsula, Mexico. Botanica Marina, 53: 195-203. doi: 10.1515/BOT. 2010.024
- Cocito, S., Bedulli, D. & Sgorbini, S. 2002. Distribution patterns of the sublittoral epibenthic assemblages on a

rocky shoal in the Ligurian Sea (NW Mediterranean). Scientia Marine, 66: 175-181. doi: 10.3989/scimar. 2002.66n2175

- Cheroske, A., Williams, S.A. & Carpenter, R.C. 2000. Effects of physical and biological disturbances on algal turfs in Kaneohe Bay, Hawaii. Journal of Experimental Marine Biology and Ecology, 248: 1-34. doi: 10.1016/s0022-0981(00)00153-2
- Coleman, M.A. 2002. Small-scale spatial variability in intertidal and subtidal turfing algal assemblages and the temporal generality of these patterns. Journal of Experimental Marine Biology and Ecology, 267: 53-74. doi: 10.1016/S0022-0981(01)00358-6
- Coleman, M.A. 2003. Effects of ephemeral algae on coralline recruits in intertidal and subtidal habitats. Journal of Experimental Marine Biology and Ecology, 282: 67-84. doi: 10.1016/S0022-0981(02)00442-2
- Connell, S.D., Foster, M.S. & Airoldi, L. 2014. What are algal turfs? Towards a better description of turfs. Marine Ecology Progress Series, 495: 299-307. doi: 10.3354/meps10513
- Cordero-Umaña, K.E. & Santidrián-Tomillo, P. 2020. Conservation status of fish and marine invertebrates of rocky reefs and sandy substrates in two unprotected bays of the Papagayo Gulf, Costa Rica. Revista de Biología Tropical, 68: 1311-1321.
- Dawson, E.Y. 1953. Marine red algae of Pacific Mexico. Part 1. Bangiales to Corallinaceae subf. Corallinoidae. Allan Hancock Pacific Expeditions, 17: 1-239.
- Dawson, E.Y. 1954. Marine red algae of Pacific Mexico. Part 2. Cryptonemiales. Allan Hancock Pacific Expeditions, 17: 241-398.
- Dawson, E.Y. 1960. Marine red algae of Pacific Mexico.Part 3. Cryptonemiales, Corallinaceae subf.Melobesioideae. Pacific Naturalist, 2: 3-125.
- Dawson, E.Y. 1961. Marine red algae of Pacific Mexico. Part 4. Gigartinales. Pacific Naturalist, 2: 191-343.
- Dawson, E.Y. 1962. Marine red algae of Pacific Mexico. Part 7. Ceramiales: Ceramiaceae, Delesseriaceae. Allan Hancock Pacific Expeditions, 26: 1-207.
- Dawson, E.Y. 1963a. Marine red algae of Pacific Mexico. Part 6. Rhodymeniales. Nova Hedwigia, 5: 437-476.
- Dawson, E.Y. 1963b. Marine red algae of Pacific Mexico. Part 8. Ceramiales: Dasyaceae, Rhodomelaceae. Nova Hedwigia, 6: 401-481.
- Edwards, M.S. & Konar, B. 2020. Trophic downgrading reduces spatial variability on rocky reefs. Scienfic Reports, 10: 18079. doi: 10.1038/s41598-020-75117-2
- Favoretto, F., Sánchez, C. & Aburto-Oropeza, O. 2022. Warming and marine heatwaves tropicalize rocky

reefs communities in the Gulf of California. Progress in Oceanography, 206: 102838. doi: 10.1016/j.pocean. 2022.102838

- García, E. 2004. Modificaciones al sistema de clasificación climática de Köppen. Universidad Nacional Autónoma de México, Ciudad de México.
- Garrabou, J., Ballesteros, E. & Zabala, M. 2002. Structure and dynamics of north-western Mediterranean rocky benthic communities along a depth gradient. Estuarine, Coastal and Shelf Science, 55: 493-508. doi: 10.1006/ecss.2001.0920
- Gauch, H. 1982. Multivariate analysis in community ecology. Cambridge University Press, Cambridge.
- Glasby, T.M., Gibson, P.T. & Cruz-Mota, J.J. 2017. Differences in rocky reef habitats related to human disturbances across a latitudinal gradient. Marine Environmental Research, 129: 291-303. doi: 10.1016/ j.marenvres.2017.06.014
- Gowan, J., Tootell, J.S. & Carpenter, R.C. 2014. The effects of the water flow and sedimentation on interactions between massive *Porites* and algal turf. Coral Reefs, 33: 651-663. doi: 10.1007/s00338-014-1154-1
- Harris, J., Lewis, L.S. & Smith, J.E. 2015. Quantifying scales of spatial variability in algal turf assemblages on coral reefs. Marine Ecology Progress Series, 532: 41-57. doi: 10.3354/meps11344
- Hay, M.E. 1981. The functional morphology of turfforming seaweeds: persistence in stressful marine habitats. Ecology, 62: 739-750. doi: 10.2307/1937742
- Hill, M.O. & Gauch, H.G. 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio, 42: 47-58. doi: 10.1007/BF00048870
- Hoffmann, J.J.L., Michaelis, R., Mielck, F., Bartholomä, A. & Sander, L. 2022. Multiannual seafloor dynamics around a subtidal rocky reef habitat in the North Sea. Remote Sensing, 14: 2069. doi: 10.3390/rs14092069
- Irving, A.D. & Connell, S.D. 2002. Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal *versus* invertebrate dominated assemblages. Marine Ecology Progress Series, 245: 83-91. doi: 10.3354/meps245083
- Kelaher, B.P. & Castilla, J.C. 2005. Habitat characteristics influence macrofaunal communities in coralline turf more than mesoscale coastal upwelling on the coast of Northern Chile. Estuarine, Coastal and Shelf Science, 63: 155-165. doi: 10.1016/j.ecss.2004.10.017
- Kendrick, G. 1991. Recruitment of coralline crusts and filamentous turf algae in the Galapagos archipelago: effect of simulated scour, erosion and accretion.

Journal of Experimental Marine Biology and Ecology, 147: 47-63. doi: 10.1016/j.ecss.2004.10.017

- León-Tejera, H. & González-González, J. 1994. New reports of macroalgae from the coast of Oaxaca, Mexico. Botanica Marina, 37: 491-494. doi: 10.1515/ botm.1994.37.6.491
- López, N. 1993. Caracterización de la ficoflora sublitoral de Acapulco y Zihuatanejo, Gro. Bachelor Thesis, Universidad Nacional Autónoma de México, Ciudad de México.
- López, N. 1996. Comunidades de macroalgas submareales de la Costa Grande de Guerrero, México. Master's Thesis, Universidad Nacional Autónoma de México, Ciudad de México.
- López, N., Rodríguez, D. & Candelaria, C. 2004. Intraspecific morphological variation in turf-forming algal species. Universidad y Ciencia, 1: 7-15.
- López, N., Candelaria, C., Ramírez-García, P. & Rodríguez, D. 2017. Structure and temporal dynamic of tropical turf-forming macroalgal assemblages of the western coast of Mexico. Latin American Journal of Aquatic Research, 45: 329-340. doi: 10.3856/vol45issue2-fulltext-9
- López, N., Rodríguez, D., Candelaria, C. & González-González, J. 2000. Subtidal macroalgal communities in Acapulco and Zihuatanejo, México. In: Munawar, M., Lawrence, S.G., Munawar, I.F. & Malley, D.F. (Eds.). Aquatic ecosystems of Mexico: status and scope. Backhuys Publishers, Leiden, pp. 335-351.
- Martinez, A.S., Dafforn, K.A., Johnston, E.L., Filippini, G., Potts, J. & Mayer-Pinto, M. 2022. Variations in benthic fluxes of sediments near pier pilings and natural rocky reefs. Marine Environmental Research, 177: 105640. doi: 10.1016/j.marenvres.2022.105640
- Martins, G.M., Hipolito, C., Parreira, F., Prestes, A.C.L., Dionísi, M.A., Azevedo, J.M.N. & Neto, A.I. 2016. Differences in the structure and functioning of two communities: frondose and turf-forming macroalgaldominated habitats. Marine Environmental Research, 116: 71-77. doi: 10.1016/j. marenvres.2016.03.004
- Mateo-Cid, L.E. & Mendoza-González, A.C. 2012. Algas marinas bentónicas de la costa noroccidental de Guerrero, México. Revista Mexicana de Biodiversidad, 83: 905-928. doi: 10.7550/rmb.28104
- Mendoza-González, A.C. & Mateo-Cid, L.E. 1998. Nuevos registros de algas marinas para Oaxaca, México. Polibotánica, 4: 54-74.
- Mendoza-González, A.C., Mateo-Cid, L.E. & Galicia-García, C. 2011. Integración florística de las algas marinas de la costa sur de Jalisco, México. Revista Mexicana de Biodiversidad, 82: 19-49.

- Mendoza-González, A.C., Mateo-Cid, L.E., Alvarado-Villanueva, R., Sotelo-Cuevas, F., Ceballos-Corona, J.G.A. & Garduño-Acosta, A.G.A. 2018. Nuevos registros y lista actualizada de las algas verdes (Chlorophyta) del litoral de Michoacán, México. Revista Mexicana de Biodiversidad, 89: 971-985. doi: 10.22201/ib.20078706e.2018.4.2604
- Piazzi, L. & Cinelli, F. 2001. Distribution and dominance of two introduced turf forming macroalgae on the coast of Tuscany, Italy, Northwestern Mediterranean Sea concerning different habitats and sedimentation. Botanica Marina, 44: 509-520. doi: 10.1515/BOT. 2001.057
- Piazzi, L., Balata, D., Pertusati, M. & Cinelli, F. 2004. Spatial and temporal variability of Mediterranean macroalgal coralligenous assemblages in relation to habitat and substratum inclination. Botanica Marina, 47: 105-115. doi: 10.1515/BOT.2004.010
- Piazzi, L., Pardi, G., Balata, D., Cecchi, E. & Cinelli, F. 2002. Seasonal dynamics of a subtidal North-Western Mediterranean macroalgal community in relation to depth and substrate inclination. Botanica Marina, 45: 243-252. doi: 10.1515/BOT.2002.023
- Portugal, A.B., Lopes-Carbalho, F., De Oliveira-Soares, M., Antunes-Horta, P. & De Castro-Nunes, J.M. 2017. Structure of macroalgal communities on tropical rocky shores inside and outside a marine protected area. Marine Environmental Research, 130: 150-156. doi: 10.1016/j.marenvres.2015.12.003.
- Prathep, A., Marrs, R.H. & Norton, T.A. 2003. Spatial and temporal variations in sediment accumulation in an algal turf and their impact on associated fauna. Marine Biology, 142: 381-390. doi: 10.1007/s00227-002-0940-4
- Rodríguez, D., López, N. & González-González, J. 2008. Gelidiales (Rhodophyta) en las costas del Pacífico mexicano con énfasis en las especies tropicales. In: Sentíes, G.A. & Dreckmann, E.K. (Eds.) Monografías ficológicas. Universidad Autónoma Metropolitana -Universidad Autónoma de Baja California, Baja California, pp. 27-74.
- Salcedo-Martínez, S., Green, G., Gamboa-Contreras, A. & Gómez, P. 1988. Inventario de macroalgas y macroinvertebrados bénticos presentes en áreas rocosas de la región de Zihuatanejo, Guerrero, México. Anales del Instituto de Ciencias del Mar y Limnología, 15: 73-96.

Received: April 7, 2021; Accepted: October 17, 2022

- Santander-Monsalvo, J., Espejel, I. & Ortiz-Lozano, L. 2018. Distribution, uses, and anthropic pressures on reef ecosystems of Mexico. Ocean & Coastal Management, 165: 39-51. doi: 10.1016/j.ocecoaman.2018.08. 014
- Short, J.A., Pedersen, O. & Kendrick, G.A. 2015. Turf algal epiphytes metabolically induce local pH increase, with implications for underlying coralline algae under ocean acidification. Estuarine, Coastal and Shelf Science, 164: 463-470. doi: 10.1016/j.ecss.2015. 08.006
- Spector, M. & Edwards, M.S. 2020. Species-specific biomass drives macroalgal benthic primary production on temperate rocky reefs. Algae, 35: 237-252. doi: 10.4490/algae.2020.35.8.19
- Steneck, R.S. 1986. The ecology of coralline algal crusts: convergent patterns and adaptative strategies. Annual Review of Ecology and Systematics, 17: 273-303.
- Steneck, R.S. & Dethier, M.N. 1994. A functional group approach to the structure of algal-dominated communities. Oikos, 69: 476-498. doi: 10.2307/ 3545860
- Sura, S., Delgadillo, A., Franco, N., Gu, K., Turba, R. & Fong, P. 2019. Macroalgae and nutrients promote algal turf growth in the absence of herbivores. Coral Reefs, 38: 425-429. doi: 10.1007/s00338-019-01793-w
- Taylor, W.R. 1945. Pacific marine algae of the Allan Hancock Expeditions to the Galapagos Islands. University of Southern California Press, Los Angeles.
- Ulate, K., Sánchez, C., Sánchez-Rodríguez, A., Alonso, D., Aburto-Oropeza, O. & Huato-Soberanis, L. 2016. Latitudinal regionalization of epibenthic macroinvertebrate communities on rocky reefs in the Gulf of California. Marine Biology Research, 12: 389-401. doi: 10.1080/17451000.2016.1143105
- Virgilio, M., Airoldi, L. & Abbiati, M. 2006. Spatial and temporal variations of assemblages in a Mediterranean coralligenous reef and relationships with surface orientation. Coral Reefs, 25: 265-272. doi: 10.1007/ s00338-006-0100-2
- Wallenstein, F.M., Neto, A.I., Álvaro, N.V. & Santos, C.I. 2008. Algae-based biotopes of Azores (Portugal): spatial and seasonal variation. Aquatic Ecology, 42: 547-559. doi: 10.1007/s10452-007-9134-y
- Wernberg, T. & Connell, S.D. 2008. Physical disturbance and subtidal habitat structure on open rocky coasts: Effects of wave exposure, extent and intensity. Journal of Sea Research, 59: 237-248. doi: 10.1016/j.seares. 2008.02.005